INVESTIGATING INDIRECT ANTHROPOGENIC EFFECTS ON SPATIAL VARIATION IN NEST PREDATION RISK AND SHOREBIRD NEST SUCCESS IN CHURCHILL, MANITOBA

TAYLOR BROWN

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Abstract

Nest predation risk increases at lower latitudes, and some shorebirds nesting at the southernmost limits of their ranges in Churchill, Manitoba tend to experience lower nest success than those at other Arctic sites. This study investigates whether proximity to human settlement affects predation risk, predator abundance and shorebird daily nest survival near Churchill by measuring these variables at varying distances from town. Camera traps at nests confirmed that foxes were important nest predators. A nest's distance to town was negatively correlated with its distance to the nearest fox den. Predation risk decreased as distances from fox dens and Parasitic Jaeger nests increased, and at high abundances of avian predators. Shorebird daily nest survival tended to be lower near fox dens and higher with a camera present. Overall, these results suggest that shorebirds may benefit from proximity to town due to reduced fox denning activity close to town.

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INTRODUCTION:

Recruitment of juvenile organisms to the breeding adult population is a key process in population dynamics (e.g. Baltazar-Soares et al. 2014). In birds, nest survival, defined as the survival of at least one egg in a clutch until hatch, is a critical step in ensuring that reproductive effort results in recruitment of juvenile individuals to the breeding population. Factors that influence nest survival, such as nest predation, may have an important impact on population size and distribution (Pienkowski 1984; Liebezeit et al. 2009). For example, nest predation pressure on Ringed Plover (*Charadrius hiaticula*) in Europe increases further south and appears to thereby define southern limits of their breeding distribution by minimizing juvenile recruitment (Pienkowski 1984).

Nests are of vital importance to avian reproduction and take a myriad of forms according to the needs of a species. Nests may be constructed in burrows underground, in rock crevices, in shallow dirt depressions, inside excavated tree trunks, or even as saliva- or mud-bound cups attached to vertical surfaces (Collias 1964). Regardless of structure and composition, nests universally function to hold, support, and often insulate eggs and chicks; and to shelter them from adverse weather conditions and potential predators. Nests, and the eggs they contain, face an array of threats over the duration of incubation. Some threats are related to parental limitations, such as inability to continue incubation during adverse weather or when disturbed (Smith and Wilson 2010; Smith et al. 2012). Other threats are directly linked to the inherent vulnerability of eggs, including brood parasitism (e.g. Payne 1977; Pöysä 1999), trampling (e.g. Paine et al. 1996), and predation (Larsen and Moldsvor 1992; Dowding and Murphy 2001; Bêty et al. 2002; Ballantyne and Nol 2011; Borgmann et al. 2013).

Egg predation is consistently found to be the leading cause of nest failure, whereby a nest fails to produce any chicks (Ricklefs 1969; Page et al. 1983; Nilsson 1984; Montgomerie and Weatherhead 1988; Larsen et al. 1996; Smith et al. 2007a; Smith et al. 2012). Egg predation may be executed by terrestrial or avian predators, or even conspecifics (Davis and Dunn 1976; Nol and Brooks 1982; Larsen et al. 1996; Dowding and Murphy 2001). Many predators that eat bird eggs do so opportunistically (Elmhagen et al. 2000; Bêty et al. 2002; McKinnon et al. 2013). Some predators may develop search images and increase nest searching effort after successful nest predation events (Byrkjedal 1989; Smith and Wilson 2010; Smith et al. 2012), but this hypothesis is not unanimously supported (Borgmann et al. 2013).

Regardless of the strategy, the rewards to egg predators are high: eggs are a highly nutritious, energy-dense food (Careau et al. 2008). Since eggs are also physiologically expensive for birds to produce (Monaghan and Nager 1997), predation poses risks to the reproductive success of nesting birds and the eventual level of recruitment. In response, birds may select nest sites strategically to reduce the risk of predation (Nilsson 1984; Tieleman et al. 2008). Among birds, shorebirds (which nest on the ground) exhibit some of the most elaborate and diverse defence behaviours ranging from cryptic concealment tactics to active predator attacks, which vary with type of parental care, adult body size, nest habitat, and incubation duration (Sordahl 1981; Larsen et al. 1996; Smith et al. 2012). Effectiveness of defence behaviours depends on the species, the predator, and the foraging strategies of the predator (Montgomerie and Weatherhead 1988; Byrkjedal 1989; Larsen et al. 1996). Aggressive nest defence behaviours such as alarm calls, direct attacks, and distraction displays entail potential survival costs to adults while increasing short-term reproductive success, while crypticity can also prevent nest predation but is

relatively neutral in terms of risk to adult survival (Montgomerie and Weatherhead 1988; Smith et al. 2007b; Smith and Edwards 2018).

Defence behaviours also vary within a given shorebird species (Smith and Wilson 2010). Shorebirds may employ different nest defence strategies according to the predator involved, usually distinguishing between mammalian (ground-dwelling) and avian predators, or between large and small predators (Byrkjedal 1989). For example, American Golden-Plovers (*Pluvialis dominica*) may show cryptic responses to avian predators (e.g. squatting still on the nest) and conspicuous responses to ground predators (e.g. distraction displays). Whimbrels (*Numenius phaeopus*) and Hudsonian Godwits (*Limosa haemastica*) are generally highly aggressive toward potential nest predators, especially avian predators, but the effectiveness of these behaviours, especially against Common Ravens (*Corvus corax*), is dubious (Byrkjedal 1989; Ballantyne and Nol 2011). It has been observed that, of 32 Palearctic shorebird species with known anti-nest predator strategies, none employed conspicuous ground predator strategies unless they employed aggressive strategies against avian predators (Byrkjedal 1989). Shorebirds may employ these differential anti-nest predator strategies based upon the relative threat that each one poses to the nest, as determined by the predator's levels of mobility and armament (Montgomerie and Weatherhead 1988).

For Arctic-nesting shorebirds, the primary cause of nest failure is nest predation (Nol and Brooks 1982; Page et al. 1983; Skeel 1983; Smith et al. 2007a; Smith 2009; McKinnon et al. 2010; Smith and Wilson 2010; Ballantyne and Nol 2011). Predation risk on ground nests declines with increasing latitude; thus, birds nesting in the low Arctic are exposed to a relatively higher risk of predation than those nesting further north (McKinnon et al. 2010). Indeed, some shorebirds suffer unusually high rates of nest predation in Churchill, Manitoba, one of the

southern-most nesting sites of Arctic- and subarctic-nesting shorebirds (Jehl 1971; Ballantyne and Nol 2011). Some species have become scarce or have stopped nesting in the area altogether, but the cause of these losses is unknown (Smith et al. 2006; Jehl 2007). However, a great diversity of shorebird species still nest in this apparently risky subarctic habitat and continue to successfully produce offspring.

Many factors influence rates of nest predation among Arctic-nesting shorebirds. For example, longer incubation breaks and nest exposure times result in higher nest predation risk, which may mean greater risk for uniparentally incubating species (Smith et al. 2012). Biparentally incubating species tend to experience higher nest success over time within a breeding season as their nest defence behaviour intensifies, as compared with uniparentally incubating species, which appear to rely more on crypticity in avoiding nest predation (Smith and Wilson 2010). In some areas, predation on shorebird nests may also be influenced by interannually fluctuating populations of preferred prey such as lemmings (*Lemmus* and *Dicrostonyx* spp.), or by seasonal flux in availability of alternative prey such as goose eggs (primarily Snow Goose *Anser caerulescens*; Smith 2009; McKinnon et al. 2013; McKinnon et al. 2014). Near human settlement, human activity can influence the activity or increase the density of opportunistically scavenging predators and increase rates of nest predation (NRC 2003; Liebezeit et al. 2009).

Over the past few decades, Arctic and subarctic predator populations have experienced considerable and rapid ecological change (Jehl 2004; Post et al. 2009; Elmhagen et al. 2017). Red foxes (*Vulpes vulpes*) are establishing populations further north throughout the Arctic, displacing Arctic foxes (*Vulpes lagopus*) and changing predator-prey dynamics (Post et al. 2009). The geographic range of ravens has expanded northward and numbers (according to

Christmas Bird Counts) in the Churchill area have increased by ~600% since the 1960s alone (Jehl 2004). A larger and still increasing number of Herring Gull breeding pairs have also been observed near Churchill from the 1990s onward (Jehl 2004). The underlying causes of these changes are multifactorial but are driven at least in part by climate change and anthropogenic alteration of habitat and food availability (Post et al. 2009; Selås et al. 2010; Stickney et al. 2014; Elmhagen et al. 2017).

OBJECTIVES, HYPTOHESES AND PREDICTIONS:

The purpose of this study is to examine how proximity to human settlement affects predator abundance, predation risk, and nest survival of five shorebird species nesting near Churchill, Manitoba. The specific objectives of my research are to: 1) quantify spatial variation in predation risk using artificial nest experiments; 2) estimate nest survival rates for five shorebird species; and 3) identify nest predators and determine their relative contribution to shorebird nest depredation rates.

HYPOTHESIS: I hypothesize that spatial variation in predator abundance, predation risk, and shorebird nest survival are affected by anthropogenic disturbance in the form of settlement in Churchill, Manitoba.

Prediction 1: Potential nest predators will be more abundant in areas closer to human settlement.

Prediction 2: Predation risk will be higher in areas closer to human settlement. I further predict that birds will be the predominant predators of artificial nests, which are visible from the air.

Prediction 3: Nest survival of real shorebird nests will be lower in areas closer to human settlement and increase with increasing distance from settlement. I further predict that mammals will be the predominant nest predators of real nests, which are usually covered by an incubating parent and therefore not visible from above.

METHODOLOGY:

Study site and system:

This study was conducted near Churchill, Manitoba which is situated on the northeastern coast of Manitoba within the subarctic region, where the mouth of the Churchill River flows into western Hudson Bay (58.768410° N, 94.164963° W; Figure 1). This subarctic site is characterized by a transition between tundra in the north and spruce-tamarack boreal forest in the south. Poor drainage, permafrost, and shallow water bodies define this region, also part of the Hudson Bay Lowlands (Skeel 1983). The Churchill area is a transition zone that hosts numerous habitat types but has been experiencing northward encroachment of woody plants in the last several decades, presumably due to climate change (Skeel 1983; Brown et al. 2007; Post et al. 2009; Ballantyne and Nol 2015).

My study area encompassed four distinct study plots located between 6.5 and 21.6 km from the town of Churchill and 1.5 – 13 km apart from each other (Figure 2). Three of these plots were 1 x 2 km (area 2 km^2) in dimensions; due to topographical limitations, one plot was 4 km x 500 m (area 2 km^2) in dimensions. Study plots represented a linear gradient of proximity to human settlement as they were located between 6.5 and 21.6 km east of the town of Churchill, which allowed for spatial analysis of predation risk and nest survival in relation to human settlement. This study area was chosen in part due to the high diversity of breeding shorebirds and high nest density in summer. The subarctic offers high-quality breeding habitat (wet; prey-dense; open landscape) at the southernmost parts of many shorebird species' breeding ranges (Skeel 1983).

Study species:

I investigated spatial variation in nest survival in a community of subarctic nesting shorebirds including Dunlin (*Calidris alpina*), Short-billed Dowitcher (*Limnodromus griseus*), American Golden-Plover, Hudsonian Godwit, and Whimbrel nesting near Churchill, Manitoba (Table 1). These species exhibit a gradient of nest defence behaviours ranging from cryptic concealment tactics to aggressive predator attacks. Shorebirds (Charadriiformes: Charadrii) are a paraphyletic group of small (20 – 700 g; Nebel and Cooper 2008; Nol and Humphrey 2012), non-perching birds commonly found along shorelines of lakes, streams and bays, and include sandpipers, plovers, curlews, and phalaropes, among others (Donaldson et al. 2000; Baker et al. 2007). Many shorebird species are highly migratory, breeding in the circumpolar Arctic and migrating as far as -55º latitude to spend the non-breeding season (Elliot et al. 1976; Myers et al. 1990; Battley et al. 2012). Shorebird species that breed in the Canadian Arctic typically migrate to the southern coastal United States, central America, the Caribbean, and throughout South America, while a few species winter in Europe or eastern Asia (Morrison 1984; Studds et al. 2017).

The mating systems of shorebirds range from polyandry to monogamy to polygamy, and parental care may be uniparental (male or female) or biparental (Warriner et al. 1986; Lank et al. 2002; Smith et al. 2007a; Smith et al. 2012). Nest defence and antipredator behaviours are common among shorebirds (Byrkjedal 1989; Larsen and Moldsvor 1992; Smith and Wilson 2010; Smith et al. 2012). Non-aggressive shorebirds have been observed nesting in proximity to more aggressively defensive nesting species as a sort of "protective umbrella" for their own nests (e.g. timid Bar-tailed Godwits *Limosa lapponica* and aggressive Whimbrels; Larsen and Moldsvor 1992; Semipalmated Plovers *Charadrius semipalmatus* and aggressive, colonial Arctic

Terns *Sterna paradisaea*; Nguyen et al. 2006; or Red Phalaropes *Phalaropus fulicarius* and aggressive, colonial Sabine's Gulls *Xema sabini*; Smith et al. 2007b).

Numbers and diversity of shorebirds nesting in the Churchill area have changed in the decades since record-keeping began. Following the completion of the railroad to Churchill in 1929 and subsequent development of infrastructure, Allen (1945) noted an increase in Whimbrels, Short-billed Dowitchers and Hudsonian Godwits but a decrease in Stilt Sandpipers (*Calidris himantopus*). American Golden-Plovers appeared to have increased in Churchill following a North American ban on hunting, but still fluctuate from year to year (Jehl 2004). Whimbrels have declined in the Churchill area and experience high rates of egg and nest failure but persist in slightly altered distributions (Jehl 2004; Ballantyne and Nol 2011). Nests of Hudsonian Godwit are difficult to find but Jehl (2004) postulated that there may have been 50-55 nesting pairs in the Churchill area in the early 2000s. However, in three years of study near Churchill between 2009 and 2011, only 57 godwit nests were found and monitored (Senner 2016); this may explain the low detection rate of godwit nests in my study. Least Sandpipers, Stilt Sandpipers, and Dunlin in the area have similarly declined in abundance in recent decades, with unclear causes. All focal species in this study nest roughly between the beginning of June and the first or second week of July, with failed breeders departing in July (Jehl 2004).

Predator abundance:

The potential shorebird nest predator assemblage in Churchill is known to include Arctic foxes (Bahr 1989), red foxes (Skeel 1983), Parasitic Jaegers (*Stercorarius parasiticus*; Byrkjedal 1989), Herring Gulls (*Larus argentatus*; Byrkjedal 1989; Jehl 2004), Common Ravens

(Ballantyne and Nol 2011), Northern Harriers (*Circus hudsonius*; Byrkjedal 1989) and Sandhill Cranes (*Antigone canadensis*; Reynolds 1985). Due to the nature of the study plots and limitations in time and number of personnel, predator surveys were conducted concurrently with other field research activities. For each visit to a study plot, one person was the designated predator counter. The survey began immediately upon the observer arriving at the plot, and the survey ended when the observer departed the plot. The observer recorded any observations of potential predators in that plot. The observer also recorded the time and date of such observations and the approximate distance from the observer to each individual predator. Individual predators that were thought to have been seen previously during the survey were either not noted again or noted again but with a comment stating it was likely a duplicate observation. These duplicate observations were usually only noted if the predator was being mobbed by a focal shorebird species or any other avian species but were not included in estimates of predator abundance.

As an index of predator abundance, we calculated the number of predators observed per hour during each survey as the total number of predators observed during a survey period, divided by the total number of hours during that survey period. The average number of predators across all surveys was then calculated per species and all species combined for each plot.

Predation risk and artificial nests:

Artificial nest experiments were biphasic: one round of deployment and monitoring occurred during "early incubation" between 11-25 of June, and one during "late incubation", 2-15 of July. At the beginning of each of these periods, 25 artificial nests were deployed in each of the four 2 km² plots, at least 150 m apart, for a total of 100 nests in each of the two rounds of experiments (density of 12.5 nests/km²). The relatively low density was used in an effort to

negate any effect of nest density on nest predation rates. The boundaries of each 2 km² plot were first delineated and drawn onto a map in Garmin Ltd's GPS unit-compatible program BaseCamp (ver. 4.6.2) using the route-drawing tool. Lines were then drawn at every 500 m along the long axis of the plot, dividing it into four equal-sized rectangular quadrats. To ensure each nest would be located at least 150 m from any other, a line was drawn 150 m in from the side of the plot (or from the previous nest) on one of the transect lines, and then a random distance between 0-500 m from that transect line was generated in Excel using the RANDBETWEEN function. If a nest from one transect line was too close to one from another transect line, another random distance value was generated. This process was repeated on each transect line but starting from the opposite side of the plot as the previous transect line.

Artificial nest cups were crude depressions stomped in the ground, roughly 7 cm in diameter. A nail with a small piece of fluorescent flagging tape was pushed into the centre of each nest cup so that the nail head was flush with the bottom of the nest; it was then concealed by the eggs but aided searchers in relocating the nest when eggs were depredated. Four clean Japanese quail (*Coturnix japonica*) eggs, which are similar to shorebird eggs in size, colour, and pattern, were placed with gloved hands in each artificial nest. Two popsicle sticks or natural markers (sticks, feathers) were placed at 5 and 10 m from the nest, respectively, or each at 5 m from the nest on opposite sides.

Each artificial nest was visited five times following deployment: once every two days, over a duration of 10 days, at which time any remaining eggs and nest markers were collected. At each visit, nest status was recorded as either: 1) nest intact; or 2) predated (at least one egg missing). Further, in the event of nest predation, any evidence of nest remains was recorded to help identify if the predator was mammalian or avian. For example, foxes will sometimes urinate

or defecate in the nest cup after emptying its contents, and avian predators sometimes pierce eggs to eat their contents but leave the shells nearby (but see Liebezeit and Zack 2008). In conjunction with motion-sensor camera photos from some nests (see below), the dates and times of nest predation events were determined as precisely as possible, and predators were identified. If a nest was depredated in the first round of artificial nest experiments, its location during the second experiment was moved by approximately 10 m to avoid habituation of predators.

Three artificial nests were excluded from analyses because their fates could not be determined due to observer error, leaving 197 nests that were used in analyses.

Nest survival:

Shorebird nests were located by two to three people, walking approximately 25 m apart through appropriate nesting habitat to flush adult birds from their nests. Once an adult was flushed, the observers stopped, moved away if necessary, and watched as the bird returned to its nest. Most nest searching effort was concentrated in early to mid-June, which is the typical nest-building and early laying stage of most shorebirds in the area (Nol et al. 1997; Jehl 2007). To prevent odour contamination of nests, searchers did not kneel, sit, or place any equipment within 15 m of the nest; nitrile gloves were worn when touching eggs and nests; and no food was consumed in the vicinity of a nest.

When a nest was found, its location was recorded in a handheld Global Positioning System (GPS) unit (Garmin Ltd., Kansas, U.S.A.) for future reference, and two popsicle sticks or natural markers (sticks, feathers) were placed at 5 m and 10 m from the nest, respectively, or

each at 5 m from the nest on opposite sides. The date and time of the visit, behaviour of attending parent(s), if parent(s) were banded and if so, the band colour combination, number of eggs in the nest, and clutch status (warm, cold, cracking, pipped, depredated, hatched) were also recorded at each visit.

Five out of nine Dunlin nests were monitored with temperature loggers as part of another study, but nest temperature data were used to confirm dates and times of predation events or hatching for this study. When a Dunlin nest was found with eggs present, a Tiny Tag temperature logger (Gemini Data Loggers Ltd; Chichester, UK) was deployed at the nest. Multiple studies have monitored shorebird nest survival using temperature probes and data loggers and have found no effect of these devices on nest survival (MacDonald and Bolton 2008; Smith et al. 2012). The temperature probe was first affixed to the end of a 10-20 cm long wooden skewer. While wearing gloves, the eggs were then removed from the nest to avoid damage as the skewer, with probe skyward, was inserted in the ground in the centre of the nest cup. It was inserted such that the probe would contact the brood patch of the incubating adult, which is approximately level with the tops of the eggs. The eggs were then replaced in their original configuration with the probe at the centre. The data logger, a small box attached to the temperature probe via a cable, was hidden ~20 cm from the nest under vegetation. The connecting cable was hidden by cutting a shallow trench through the soil and vegetation and inserting the cable, and then lightly burying it with the displaced soil and vegetation. Tiny Tags were replaced every 11 days, which is the length of their battery life, and removed when nest fate was ascertained.

During the initial visit to a nest (when found), 2-4 of the eggs were floated if the ambient temperature was above freezing, to determine incubation start date and expected hatch date (Liebezeit et al. 2007). Eggs were placed in a plastic container with pre-drawn compass angles

and a millimetre scale and filled with tepid (~21ºC) water. Eggs were then placed back into the nest in their original configuration. Only two eggs per nest were floated in this manner, unless the angles at which they floated were very different, upon which a third and possibly a fourth egg were floated. All eggs were measured in length and width to the nearest 0.01 mm using digital calipers (Fowler High Precision, Inc., Massachusetts, USA).

Nests were checked every four days for predation or hatching events and, in the case of Dunlin nests, to make sure the Tiny Tag was still in position and with battery life remaining. Motion-sensor nest cameras (protocol details follow) were also checked at these intervals. When the expected hatch date of a nest was near and/or if eggs were found cracked or pipped, visits were made more frequently (every 1-2 days) to determine the exact date of hatch. In the event of a nest check where eggs were missing, any signs of nest fate were recorded including presence of chicks, parent behaviour, eggshell pieces or fragments, fox urine smell, or dislodged nest material. In conjunction with estimated hatch date and/or Tiny Tag data and/or camera trap photos, nest fate was ascertained as successful (at least one egg hatched), failed (no eggs hatched), or unknown.

Nest predator identification:

Motion-sensor cameras (Reconyx PC900 and Reconyx Hyperfire 2: Holmen, Wisconsin, USA; Moultrie A-25i: Calera, Alabama, USA) were installed at 47 of 200 (23.5%) artificial nests and at 16 of 50 (32%) real shorebird nests to identify nest predators and to discern if there was any effect of cameras on predation risk or nest survival, respectively. In addition, one camera trap was randomly placed in each plot in order to provide an index of predator activity that

covered the entire 24-hour period. Cameras were camouflaged with vegetation and placed 5 m away from the nests on small tripods lying on the ground or, if no dry ground was available, standing 0.5 m tall. Randomly-placed cameras were not camouflaged and stood 0.5 m tall. Cameras took a rapid series of five photographs each time the built-in Passive InfraRed (PIR) motion sensor was triggered by movement within its field of view. Eggs in real and artificial nests were not conspicuous enough to be seen in camera photos taken at distances of 5 to 10 m, so the installer triggered the camera to take a calibration photo of them pointing to the nest. Cameras were checked every four days (coordinated with regularly scheduled nest checks described above), and batteries and SD cards were replaced if necessary.

McKinnon and Bêty (2009) used camera traps at artificial and real shorebird nests and found no evidence of camera effects on predation risk or nest survival, but this study was conducted at a higher latitude and with different shorebird species than those found nesting in Churchill. There was similarly no evidence suggesting that cameras increase shorebird nest predation in New Zealand or on Lapwing (*Vanellus vanellus*) nests in the United Kingdom (MacDonald and Bolton 2008). In order to test for an effect of cameras on real and artificial nests in our study, cameras were placed randomly at a maximum of 50% of the artificial nests monitored. For real nests, cameras were placed at every second nest of each species as soon as they were found. They remained at the nests until the chicks hatched or the nest failed.

Predator visits were categorized as confirmed predation events, uncertain, or non-predation events. If a predator was photographed with eggs in its mouth, or without eggs in its mouth but with its head in the nest and the nest was then found to be depredated, it was considered a predation event. If a predator was photographed within the vicinity of the nest but without its head in the nest or eggs in its mouth, and the nest was then found to be depredated, it

was considered a possible but unconfirmed predation event. If there was evidence that all eggs were already removed when photographs were captured of a predator with its head in the nest, it was considered a possible but unconfirmed predation event. If a predator was photographed in any position and the nest was then found to be intact, or if the predator was only visible at a distance from the nest, it was considered a non-predation event.

Proximity to predator nests and dens:

Distance to nearest jaeger nest and distance to nearest fox den were both identified post-hoc as potential covariates to explain spatial variation in predation risk and/or rates of nest survival. Locations of Parasitic Jaeger nests were saved in GPS units when found incidentally in each of the study plots, and the distance from each artificial and real nest to the closest jaeger nest was measured using the straight-line measuring tool in Google Earth Pro (ver. 7.3.2.5776). The locations of all red and Arctic fox dens monitored in 2018 were provided by Dr. Jim Roth, along with the following information for each den: number of burrows cleared out; presence of fox tracks; presence of fresh feces; presence of urine odor; presence of fresh prey; and presence of shed fox hair. For the purposes of this study, only dens monitored in June (at the time of nest experiments and shorebird nesting) were considered, and only dens with a) at least one burrow cleared out, *and* b) one other evidence of fox activity, were considered active. Fox den locations were mapped on Google Earth Pro and the distance from each artificial and real nest to the closest fox den was measured using the straight-line measuring tool.

Data Analysis:

Predator Abundance:

To determine if mean predator abundance significantly differed among plots, a Kruskal-Wallis test was conducted in program R (ver. 3.5.3) because data were not normally distributed. To test for a difference in mean predator abundance between the early and late incubation periods, an unpaired Mann-Whitney U test (Wilcoxon rank sum test) was conducted. Proportions of predator species seen in each plot were tested for significant differences using a Chi-square test. All statistical tests were then repeated for the dataset excluding Herring Gulls and foxes. Herring Gulls were excluded from final predator abundance analysis because: 1) the presence of a small breeding colony in the plot 14.5 km from town was considered a strong source of bias in the predator abundance dataset; and 2) camera trap evidence and anecdotal observations from this study indicate they make negligible contributions to shorebird nest predation, which is in agreement with previous studies in Churchill and elsewhere (Jehl 1971; Jehl 1973; Skeel 1983; Jehl 2007; Smith et al. 2007a; Ballantyne and Nol 2011; Ballantyne and Nol 2015). Foxes were also excluded from predator abundance analysis post-hoc because only one Arctic fox and zero red foxes were observed during the diurnal predator surveys. It is typical for foxes to be undercounted during diurnal surveys (Liebezeit and Zack 2008) due to their crepuscular nature (Byrkjedal 1989, Díaz-Ruiz et al. 2016). Thus, the calculated average predator abundances more accurately represented average abundance of avian predators.

Predation risk:

To test for a relationship between Kaplan-Meier survival estimates of artificial nests and explanatory variables of interest, Cox Proportional Hazards regression modelling was used (Cox 1972) with the *survival* (v.2.44-1.1, Therneau 2015) and *survminer* (v.0.4.4, Kassambara) packages in program R (v.1.2.1335). Assumptions of proportionality of survival and hazards were tested graphically (Hess 1995). I tested for correlations among the six predictor variables of interest, namely distance from town, camera presence, incubation phase (early or late), avian predator abundance, distance from nearest Parasitic Jaeger nest, and distance from nearest fox den. Distance from town and distance from nearest fox den were negatively correlated ($r = -0.48$, $p < 0.001$). Distance from town was originally considered the main predictor variable of interest; however, given the correlation with distance from nearest fox den, the use of fox den locations made more biological sense, so this variable was used hereafter.

One Parasitic Jaeger nest was located in or near each of the four study plots; however, the nest in or near the plot 14.5 km from town was never precisely located. For this plot, missing values were replaced using mean imputation based on distance to jaeger nest data for the other three plots.

Avian predator abundance was calculated as the mean number of avian predators, excluding gulls, observed per hour over the duration of the incubation period in which a given artificial nest was active, in the plot in which the nest was located.

Nest survival:

Between June 8 and July 18, 2018, 50 shorebird nests were found of seven species. Ten nests were removed from analyses due to unknown nest fate. Data for two species (Least Sandpiper and Stilt Sandpiper) were not included in analyses because of small sample sizes of three and one nests respectively. Thus, 36 nests of five species were used in analysis of nest survival (Table 2).

Species, camera presence, distance from town, avian predator abundance, distance from nearest Parasitic Jaeger nest (in metres), and distance from nearest fox den (in metres) were tested for Pearson correlation in program R. Distance from town and distance from nearest fox den were correlated ($r = -0.53$, $p < 0.01$). Distance from town was thus removed from analyses of shorebird nest survival for the same reasons described above (see Predation Risk). Also, the method of mean imputation described in the previous section was used for distance to jaeger nests for real shorebird nests located in the plot 14.5 km from town.

To test the hypotheses regarding the effects of the above covariates on daily nest survival of shorebirds, 12 nest survival models, including a null model, were constructed *a priori* from combinations of the five predictor variables (Table 3). Because predator effects were of primary interest, species and camera presence were added to only some models. Due to the small sample size of nests, covariate interactions were not tested.

Competing models were built and model selection was conducted using the Nest Survival function in program MARK (ver. 9.0; Dinsmore et al. 2002). Daily survival rate (DSR) is the probability that a given nest survives one "exposure day" of the nesting season. Program MARK models DSR using a modified version of the Mayfield method (Mayfield 1961; Mayfield 1975)

and standardizes rates of DSR using units of exposure days. The nesting season specific to this study began the day that the first nest was found (June 8), and ended the last day that any nest was checked (July 14). This nesting season was thus composed of 37 exposure days. At minimum, four pieces of information were required for each nest in building models: 1) the day of the nesting season on which the nest was found; 2) the day that the nest was last observed intact; 3) the day that the nest was last checked; and 4) the fate of the nest (0 = successful, 1 = depredated; Dinsmore et al. 2002). Nests were considered successful if at least one egg hatched. Akaike's Information Criterion for small sample sizes (AIC_c) was used to identify the top model. The best-fitting model to describe variation in nest survival was that which had the lowest ΔAIC_c value, but all models within two ΔAIC_c ($<2\ \Delta AIC_c$) from the top model were considered competitive (Burnham and Anderson 2004).

RESULTS:

Predator Abundance:

Over 169 hours of observations, 758 avian predator observations were made across all plots (Table 4). Herring Gulls, which made up 62% of observations (n = 471), were later considered non-contributing shorebird nest predators, leaving 287 observations of other species. The remaining most common potential nest predators were Common Ravens (112), Parasitic Jaegers (86), and Sandhill Cranes (70; Table 4). Individuals of six other species made up the remaining 19 observations (Table 4). The high proportion of Herring Gulls that constituted predator observations is influenced by a nesting colony in the plot 14.5 km from town. Proportions of avian predator species (including gulls) varied among plots (n = 758; Figure 3), and this variation was significant even when gulls were excluded for final analyses (n = 287, Pearson $\chi 2 = 57.167$, df = 9, $p < 0.001$; Figure 4).

There were significant differences in mean predator abundance among plots when Herring Gulls and the one fox observation were included in analyses (Kruskal-Wallis $\chi 2 = 41.76$, df = 3, $p < 0.001$; Figure 5). However, when analyses were reconducted excluding Herring Gulls and foxes, predator abundance was no longer significantly different among plots (Kruskal-Wallis $\chi 2 = 6.8155$, df = 3, $p = 0.078$; Figure 6).

Avian predator abundance was significantly higher in the early incubation phase (late June) compared to the late incubation phase (early July; W-statistic = 299.5, $p < 0.05$).

Predation Risk:

Predation risk was significantly higher in close proximity to Parasitic Jaeger nests (coefficient = -0.924, z = -3.477, SE = ±0.266, $p < 0.001$). For each additional kilometre away from a Parasitic Jaeger nest, predation risk decreased by 60.3%. Artificial nests were located on average 0.70 km (±0.33 SD, range 0.092 – 1.460) from the nearest jaeger nest. Predation risk was also significantly higher in close proximity to fox dens (coefficient = -0.287, z = -5.362, SE = ±0.054, $p < 0.0001$). For each additional kilometre away from a fox den, predation risk decreased by 25.0%. Artificial nests were located on average 2.86 km (±1.76 SD, range 0.598 – 6.230) from the nearest fox den. Increased avian predator abundance was associated with a decrease in predation risk (coefficient = -0.609, z = -3.165, SE = ±0.192, $p < 0.01$). For an average increase of one avian predator observed per hour, predation risk decreased by 45.6%. Mean avian predator abundance ranged from 0.82 – 2.87 predators per hour. The presence of a camera did not affect predation risk (coefficient = -0.244, z = -1.277, SE = ±0.191, $p = 0.202$) at artificial nests. Incubation phase also did not affect predation risk (coefficient = -0.031, z = -0.140, SE = ±0.221, $p = 0.888$).

Nest Survival:

Variation in daily nest survival was best described by a model including distance from the nest to the nearest fox den and camera presence. Daily nest survival was higher with increased distance from nearest fox den ($\beta = 0.202^{-03}$; SE = $\pm 0.126^{-03}$; Figure 7) and higher for nests with cameras ($\beta = 0.053$; SE = ±0.078) than those without ($\beta = 0.003$; SE = ±0.008).

The most competitive model included only distance from the nest to the nearest fox den (ΔAIC=0.4693). However, the null model was also competitive (ΔAIC=0.5823; Table 5) indicating that a model without variables could explain the variation almost as well as the top model.

Nest Predators:

Of 33 predation events recorded at artificial nests, 19 (58%) were by Parasitic Jaegers, seven (21%) by Arctic foxes, three (9%) by Herring Gulls, two (6%) by red foxes, one (3%) by a Common Raven, and one (3%) by a Northern Harrier (Table 6). In several cases, an artificial nest appeared to be depredated by more than one predator. For example, one artificial nest appeared to be depredated by an Arctic fox, a Parasitic Jaeger, and a Common Raven (Figure 8); one by a red fox and possibly a Parasitic Jaeger (Figure 9); one by a pair of Parasitic Jaegers and a Common Raven (Figure 10); and one by a Common Raven and an Arctic fox (Figure 11). However, in the last example we concluded that the Common Raven depredated all four eggs because there are four sequential photos showing the raven enter the field of view, take an egg into its bill, and exit the field of view. The Arctic fox may have responded to the scent left by the eggs (hence photos with its nose in the nest cup) but was not an actual predator of that nest.

Of 11 predation events recorded at real shorebird nests, four (36%) were by Arctic foxes, three (27%) by red foxes, three (27%) by Parasitic Jaegers, and one (9%) by a Northern Harrier (Table 7). In two cases, a real shorebird nest appeared to be depredated by more than one predator (Table 8). One Whimbrel nest was depredated by an Arctic fox and by a Parasitic Jaeger

(Figure 12), and an American Golden-Plover nest was depredated by a Northern Harrier and by a red fox (Figure 13).

Parasitic Jaegers and Herring Gulls were photographed pulling the flagging-taped nails out of nest cups after removing one or more eggs from artificial nests (n = 3), and nails were seen pulled from nest cups at nests without cameras as well. Parasitic Jaegers and Herring Gulls were both photographed approaching and inspecting cameras (n = 8 jaegers, n = 1 gull). Red and Arctic foxes were both photographed approaching, inspecting, and in some cases scent-marking cameras (n = 3 Arctic foxes, n = 1 red fox).

Sometimes, camera trap photos revealed the method by which a predator fed on eggs. If eggs were small enough, as in the small Japanese Quail eggs of artificial nests (or in the one Stilt Sandpiper nest which was found), Parasitic Jaegers appeared to use three different methods for feeding on them: swallowing them whole (n = 6), puncturing and lapping out the contents (n = 3), or carrying them off (n = 1). In all instances where it was possible to determine the feeding method of red and Arctic foxes on both real and artificial nests, they carried eggs off-site (presumably to cache them; n = 8).

Over a period of 3,025 camera trap hours, 12 predators triggered the four randomly-placed cameras within each plot (Table 9). Both red and Arctic foxes were photographed at artificial nests, real nests, and random locations almost exclusively during night or twilight hours (Figure 14). Only three of 30 (10.0%) encounters of foxes at camera traps were outside of the hours of 22:00 – 06:00, and of those, none appeared to be predation events. Avian predators such as Parasitic Jaegers, Common Ravens, Northern Harriers, and Sandhill Cranes were photographed at artificial nests, real nests, and random locations exclusively during daylight (or,

seldom, twilight) hours (Figure 14). However, note that Sandhill Cranes were not confirmed predators in this study. Only three of 69 (4.3%) encounters of avian predators at camera traps were outside of the hours of 06:00 – 22:00, and of those, two were predation events (both by Parasitic Jaegers). Cameras detected predators between June 14 and July 13; at the midpoint between these two dates, on June 28, 2018, sunrise in Churchill was 04:09 and sunset was 22:30.

DISCUSSION:

Human activity can influence the activity and/or density of predators and thus indirectly affect prey species (Liebezeit et al. 2009). The results from this study indicate that proximity to human settlement may indeed affect shorebird – nest predator relationships, but in the opposite direction hypothesized. I found no support for my hypothesis that predator abundance would be higher in close proximity to town. That predation risk was highest in close proximity to fox dens reveals that the nests closer to town experienced lower risk, which was opposite of that predicted. Predation risk was also highest closer to jaeger nests, but surprisingly, decreased as avian predator abundance increased. Daily nest survival of real shorebird nests was also lowest in close proximity to fox dens; however, these results must be interpreted with caution. The presence of cameras did not appear to have any negative effects on predation risk, and, surprisingly, there was even some indication of a positive effect of cameras on daily nest survival of shorebirds. As predicted, shorebird nests were most often depredated by Arctic and red foxes, which were underrepresented in abundance surveys, whereas artificial nests were most often depredated by avian predators, primarily jaegers.

Predator Abundance:

Predator abundance was expected to be higher closer to town because of the potential attractive effect of anthropogenic food sources such as pets, garbage, roadkill, and hunting- or fishing-related offal (NRC 2003; Liebezeit et al. 2009; Selås et al. 2010). Among my study plots, predator communities differed but abundance was not higher closer to town, even when the large colony of gulls located in the plot 14.5 km from town (third-farthest) was excluded from

analyses. Predator surveys revealed Herring Gulls, Common Ravens, Parasitic Jaegers, and Sandhill Cranes as the most abundant potential avian predators across all study plots, which concurs with previous studies conducted in Churchill (Skeel 1983, Byrkjedal 1989; Ballantyne and Nol 2011) and other subarctic sites (Smith et al. 2007a). On Alaska's North Slope, human infrastructure related to oil, gas, and other activities has attracted predators such as bears, foxes, ravens and gulls in higher densities due to the availability of supplemental food, which has generally caused decreases in nest success of local breeding birds, sometimes to the point of mortality being higher than recruitment (NRC 2003). Based on the results of the current study, it is uncertain whether the distribution of predators near Churchill is the exception or the rule; therefore, study of the variation in predator abundance in proximity to other Arctic and subarctic settlements should be pursued further.

Both red and Arctic foxes were relatively underrepresented in the diurnal surveys, with only one fox observation in nearly 170 hours of incidental predator surveys. Camera trap data revealed that most of the 30 fox encounters at cameras occurred between 22:00 and 06:00, which in Churchill during summer corresponds to mostly night and twilight hours. The same underrepresentation of foxes during diurnal surveys has been found in other studies in Churchill and Alaska (Byrkjedal 1989; Liebezeit and Zack 2008). Foxes are generally crepuscular and/or nocturnal in nature (Byrkjedal 1989), especially in areas (such as Churchill) where they are hunted or where human activity is high (Díaz-Ruiz et al. 2016). Although predator surveys in general are good to give an idea of predator community composition (especially avian), their diurnal bias translates to a lack of suitability for detecting foxes. As such, future studies should consider deployment of randomly-distributed camera traps as a potentially unbiased method to monitor predator activity.

The sole observation of an Arctic fox during predator surveys occurred in the third-farthest plot, 14.5 km from town. Mammalian predator activity was higher farther from town as revealed by the negative correlation between distance from a nest to town and distance from the nearest fox den, and by the higher number of active dens near the farthest plot (J. Roth, unpubl. data). This relationship is opposite what I expected based on the potential availability of food subsidies near town (NRC 2003), the willingness of red foxes to den and hunt near human settlement (Selås et al. 2010; Stickney et al. 2014), and local Arctic foxes being described as "bold" (although red foxes are more shy; J. Roth, pers. comm.) and not averse to humans (L. Fishback, pers. comm.). However, there may be fewer fox dens and less fox activity near town due to foxes being actively hunted in Churchill. Other reasons may include the efficient storage and disposal of potential food subsidies, and/or avoidance of loud aircraft traffic and air cannons at the local airport (next to the closest plot at 6.5 km). Arctic fox den use in Norway was not correlated with distance to human infrastructure (Frafjord 2003) but at one site, den use and reproductive success was higher with fewer cabins and roads nearby (Selås et al. 2010); however, in Alaska, they can commonly be found denning and hunting in highly anthropogenically-disturbed areas (NRC 2003).

Sandhill Cranes may be considered potential nest predators (Reynolds 1985; Gerber et al. 2014) despite the lack of confirmed evidence that they consume shorebird nests; as such, out of caution they were counted toward avian predator abundance since they were present in all of my study plots. It is important to note that the amount of time spent in each plot for predator surveys was not consistent (as low as 25 hours in one plot and as high as 60 hours in another), and as such mean avian predator abundance calculations may be less accurate for plots with lower effort. Indeed, standard deviation of predator abundance in the plot with 25 hours of survey time

was highest of the four plots. Also, in this study, precise estimates of breeding individuals of each predator species were not obtained, but in future work could be a better indication of predator activity.

Predation Risk:

Camera monitoring confirmed that artificial nests were depredated more often by avian (73%) as opposed to mammalian predators (27%) with Parasitic Jaegers accounting for 57.6% of confirmed predation events at artificial nests. Given these results, it was not surprising that predation risk was negatively affected by distance to jaeger nests with an impressive 60.3% decrease in predation risk with each additional kilometre away from a jaeger nest. It is thus apparent that nests near jaeger nests are not afforded the same "umbrella" of protection as when located near other aggressively defensive (but non-egg-consuming) nesting avian species (Larsen and Moldsvor 1992; Nguyen et al. 2006; Smith et al. 2007b). Parasitic Jaegers are opportunistic carnivores that prey on lemmings (*Lemmus* and *Dicrostonyx* spp.), birds and birds' eggs; the latter items sometimes form the largest proportion of their diet (MacInnes 1962; Wiley and Lee 1999; Bêty et al. 2002). Jaegers are visually-oriented avian predators that often cruise low to the ground (1-3 m) in search of prey and can learn to preferentially search areas where encountering nests is more likely (Wiley and Lee 1999). Though artificial nests are small and well camouflaged, with no incubating parent they are likely a relatively easy target for such a low-flying avian predator. On Bylot Island, Long-tailed Jaegers were responsible for the majority of artificial nest losses when lemmings were abundant (McKinnon and Bêty 2009), but at the same site and using larger eggs, Parasitic Jaegers caused the majority of egg predation and attempted

the most predation attempts on artificial nests at lowest lemming abundance (Bêty et al. 2002). It is unknown whether the low lemming densities in Churchill even at population peaks (~2 per hectare; J. Roth, unpubl. data) have any effect on predation risk by jaegers, but perhaps in areas with low densities, or low cyclicity of lemming populations, jaegers may rely on birds and birds' eggs as major food sources.

Predation risk was also negatively affected by distance to the nearest active fox den (red and Arctic foxes combined), with a 25% decrease in predation risk with each additional kilometre away from an active fox den. Arctic foxes were responsible for 21.2% of confirmed predation events at artificial nests, while red foxes were responsible for 6.1%. Den locations and the negative correlation between distance from town and distance from nearest den imply that dens are fewer, and farther from nests, near town; predation risk is therefore also lower near town, which is similar to a decrease in predation risk observed near walking trails (Miller and Hobbs 2000). Both Arctic and red foxes are thought to hunt primarily using olfactory cues (Smith et al. 2012), but as opportunistic omnivores they use any cues available to find prey such as small mammals, birds, birds' eggs, insects, and carrion (Chesemore 1968; Bahr 1989; Elmhagen et al. 2000) and may cache these items for consumption months later (Bahr 1989; Careau et al. 2008). Lemmings are the preferred prey of Arctic foxes, but bird eggs become important prey in years or locations of low lemming density (Larson 1960; Summers 1986; Martin and Baird 1988; Bahr 1989; Bêty et al. 2002; Smith et al. 2007a; McKinnon and Bêty 2009; McKinnon et al. 2014). In addition to sensory cues, Arctic foxes may stumble upon prey incidentally (McKinnon et al. 2014) or pass by it without notice if no cues are noticed, e.g. at nests where the incubating adult does not flush (Bahr 1989). On Bylot Island, Nunavut, Arctic foxes were the only confirmed predators of artificial shorebird nests in the year of low lemming

abundance (McKinnon and Bêty 2009) and predation risk increased as fox density increased (McKinnon et al. 2014).

Interestingly, Arctic foxes were only photographed depredating artificial nests in the plot located 14.5 km from town. The only visual observation of a fox during surveys was also from this plot which was home to a nesting colony of Herring Gulls, a small nesting colony of Arctic Terns, and sporadic nesting Canada Geese. The fox was observed carrying a large white egg in its mouth, presumably a goose egg, and was being actively mobbed by several Arctic Terns. This observation occurred only ~700 m from an active Arctic fox den. In another instance, a camera trap at an artificial nest in this plot photographed an Arctic fox approaching the camera at 23:49 on July 4, and again 48 hours later at 23:43, approaching from the same direction. It was only on the second visit that the fox depredated the nest. This provides anecdotal evidence that a) the camera did not attract the fox, and b) the fox loosely followed an established hunting route on consecutive days, and likely stumbled upon some artificial nests without the use of olfactory or visual cues. Photographs from cameras at other artificial nests show foxes apparently finding nests through olfaction (nose in nest cup) even after it was emptied of its contents previously by a different predator.

Surprisingly, predation risk decreased as avian predator abundance increased, though it is important to note that the avian predators represented by this variable were mostly Parasitic Jaegers (depredated 19 artificial nests, three real nests), Common Ravens (depredated one artificial nest, zero real nests), and Sandhill Cranes (did not depredate nests). This may be due to exclusion of mammalian predators by breeding avian predators, which potentially offer protection through mobbing. A similar trend was observed on Bylot Island, Nunavut, where an increase of one breeding avian predator per 100 km² resulted in a 1% decrease in predation risk

(McKinnon et al. 2014). I predicted predation risk would be highest where predators (De Santo and Willson 2001), and avian predators specifically (Ekanayake et al. 2015) were most abundant, but the influence of each predator species on predation risk may be more telling than the influence of all predators combined.

Predation risk did not decrease significantly from the early to late incubation period which contradicts findings from other studies. Reduction in snow cover in northern Norway from late May to late June was hypothesized to be the cause for a concurrent decrease in predation risk on artificial shorebird nests (Byrkjedal 1980), but in my study area in June, snow cover is negligible even at the beginning of artificial nest experiments.

Finally, camera presence did not affect predation risk in my study, which agrees with the results of camera studies on both artificial (McKinnon and Bêty 2009) and real nests (Liebezeit and Zack 2008; MacDonald and Bolton 2008). My study adds to the growing body of literature supporting the use of cameras as the best method for identifying predators at artificial and real nests.

Nest Survival:

Based on the top model, daily survival rate of shorebird nests increased with increasing distance from the nearest fox den and increased with a camera present. However, because the null model was competitive, these results should be interpreted with caution. That said, the results are consistent with the effects of fox dens on predation risk: predation risk increased in close proximity to fox dens and daily nest survival decreased. We did not find any effects of

avian predators (proximity to nests or abundance) which is coherent with the fact that foxes were the dominant predators at real nests. Jaegers were confirmed predators at three of 11 nests, which is not negligible, and models including distance to jaegers were found within 4 ΔAIC, which some studies still consider competitive, therefore the effects of jaegers on daily nest survival warrant further attention.

Arctic and red foxes were responsible for four and three of 11 photographed predation events, respectively, at real shorebird nests. Arctic foxes have often been considered unimportant predators of shorebird nests in Churchill (Byrkjedal 1989) or ignored as potential nest predators altogether (Jehl 1973; Skeel 1983; Ballantyne and Nol 2011; Ballantyne and Nol 2015), even though Arctic foxes have been observed depredating shorebird eggs at Churchill in years of both high and low lemming abundance (Bahr 1989) and they are dominant shorebird nest predators elsewhere (Liebezeit and Zack 2008). In a study on Whimbrel nest survival near Churchill, ravens were the only directly observed nest predators (Ballantyne and Nol 2011), but no ravens were photographed depredating shorebird nests in my study. Indeed, of the four predation events I documented at Whimbrel nests, three were foxes (two Arctic, one red), and one was a jaeger. It is unknown whether this lack of detection of ravens is due to true absence or due to their avoidance of cameras, but the latter seems somewhat unlikely considering they were photographed at artificial nests. A review of shorebird camera monitoring studies in Europe revealed that roughly 61% of predation events were by foxes, concluding that that the long-held belief of birds being the most prominent shorebird nest predators is "frequently not true" (MacDonald and Bolton 2008). Effects of fox density and proximity to fox dens on shorebird nest survival have now been documented in several studies in the low and high Arctic

(McKinnon and Bêty 2009; McKinnon et al. 2014; Smith et al. 2007b) and my results now confirm the importance of nest predation by foxes in the subarctic.

Shorebird nest predation by Arctic foxes is known to be influenced by lemming abundance: in a year of lower lemming abundance near Churchill, shorebird and other bird eggs constituted a higher proportion of the Arctic fox's diet (Bahr 1989). Results from other Arctic studies imply similar patterns of periodicity of shorebird nest predation by Arctic foxes according to lemming cycles, as explained by the alternative prey hypothesis (Summers 1986; Martin and Baird 1988; Bêty et al. 2002; Smith et al. 2007a; McKinnon and Bêty 2009; McKinnon et al. 2013; McKinnon et al. 2014). In areas of the Arctic where lemmings are scarce and/or their populations non-cyclic, birds and their eggs and young form large proportions of the diet of Arctic foxes (Larson 1960). Due to limitations in time and number of personnel, I could not quantify lemming abundance during my study. However, lemming populations in the Churchill region have decreased significantly in the last several decades and cycles are relatively weak (J. Roth, unpubl. data). Considering the high proportion of shorebird nests depredated by foxes in my study, the concurrent decades-long decline in nest survival of shorebirds nesting near Churchill may be caused, in part, by prey-switching of Arctic foxes.

In my study, camera trap evidence indicates that the majority of eggs from artificial and real shorebird nests were cached rather than eaten immediately by Arctic foxes. Lemmings are relatively scarce in my study area compared with population estimates in prior decades, with a peak density in 2017 of only ~2 individuals per hectare and slightly fewer in 2018 (J. Roth, unpubl. data). Thus, it is unlikely that lemming density alone is high enough anymore to account for this egg-caching behaviour, which was previously documented to occur most frequently in years of high lemming density (Bahr 1989); rather, I posit that in this system of reduced lemming

abundance, egg-caching behaviour may be anecdotal evidence of higher abundance of other prey (e.g. other bird eggs, coastal food sources, subsidized food). Any potential influence of lemming populations, however small, on shorebird nest survival and nest predator behaviour should be interpreted with caution due to the temporally limited nature of this study.

The presence of cameras at nests did not negatively affect daily survival rate in this study. These results are consistent with several other studies showing no effects of camera monitoring on shorebird nests (Liebezeit and Zack 2008; MacDonald and Bolton 2008; McKinnon and Bêty 2009). Although the results need to be interpreted with caution, the effect of cameras was actually positive; nests with cameras experienced slightly higher daily nest survival. Positive effects of camera traps have been found in other studies on real nests (Thompson et al. 1999; Herranz et al. 2002; Richardson et al. 2009). Camera presence may affect risk of predation by mammalian and avian predators differently; in one study, magpies avoided conspicuous cameras (Herranz et al. 2002), and in another Arctic foxes approached and scent-marked cameras (although this did not result in higher predation; McKinnon and Bêty 2009). It has been proposed, however, that the neophobia exhibited by mammalian and corvid predators generally means they avoid conspicuous cameras (Richardson et al. 2009). From photos captured during this study, both Arctic and red foxes appeared at times to recognize the camera as a foreign object, either by staring at it, by doing a double-take (running by and then running by again while looking at the camera), or by scent-marking the camera. Parasitic Jaegers and Herring Gulls were also photographed approaching and inspecting cameras. Although the cameras were concealed as best as possible, the terrain in my study plots was relatively flat with little woody vegetation so they were conspicuous enough for predators to see. An increase in shorebird nest survival due to cameras could be explained if foxes, the main predator, were actually distracted

enough by the cameras to miss the nest (McKinnon and Bêty 2009). In future studies, where sample sizes permit, interactive effects of camera presence and predator type should be considered.

Despite any potential effects, the importance of using cameras to identify predators cannot be denied. In a review of predation on shorebird nests in Europe, only 7.4% of predation events at nests with camera traps were unattributable to a specific predator, compared to more than 45% when using nest remains alone (MacDonald and Bolton 2008). Similarly, predators of nests monitored with camera traps in Alaska could not have been reliably identified by nest remains alone, considering nests were left intact by both foxes and jaegers, with no traces of the eggs (Liebezeit and Zack 2008). My study adds to the growing body of literature supporting the use of cameras to identify nest predators, and it would be prudent in future studies of shorebird nest survival in Churchill and elsewhere in the Arctic to use camera traps for predator identification.

Nest survival did not appear to vary by species in this study system, contrary to what has been found at other sites with other shorebird species (Smith et al. 2007a; Smith 2009; Smith et al. 2012). However, the lack of species effect may have more to do with the lack of variation in incubation system (all biparental in my study). Nests of biparental incubators are rarely left uncovered and incubating parents provide near-constant camouflage to the nest. In the case of aggressively defensive species, the parent(s) also provide active protection to the eggs. On Southampton Island, Nunavut, increased abundances of Parasitic Jaegers or Arctic foxes resulted in decreases in all shorebird species' daily nest survival, but increases in jaegers disproportionately affected nest survival of uniparental incubators and increases in foxes disproportionately affected that of biparental incubators (Smith 2009). The author postulated that

this discrepancy, and the lower overall nest survival of uniparental species, is due to increased conspicuousness as the result of a higher rate of incubation recesses. However, I suggest that the correlation between incubation system, nest survival rate, and predator type is more likely due to the increased conspicuousness of the eggs themselves, especially from above (Angelstam 1986; Rees et al. 2015). Artificial nests and uniparental nests are similar in their being left uncovered for long periods of time, and jaegers disproportionately affected both uniparental incubators in Smith's (2009) study and artificial nests in my study. The visual, low-flying hunting style of Parasitic Jaegers is likely particularly effective for spotting uncovered eggs compared to the "stumble upon and/or flush" style of foxes, which disproportionately affects nests with an incubator present but can also affect uncovered nests for an additive effect. It may be for this reason that there is only one uniparentally incubating species that breeds in the Churchill area, and numbers of this species, the Red-necked Phalarope, are small. I therefore predict that nests of Red-necked Phalaropes near Churchill experience lower nest survival than biparental incubators and suggest that future studies concentrate on discerning differential effects of foxes and avian predators on shorebirds of these two incubation types by using camera traps.

Avian predator abundance did not appear to affect daily nest survival in the five focal species I studied, although camera trap data indicated that four of 11 predation events were by avian predators. These results are consistent with other studies showing no effect of avian predator abundance on nest survival of 14 Arctic-breeding shorebird species (Weiser et al. 2018b) or on hatching success of Avocets (*Recurvirostra avosetta*) in Germany (Hötker and Segebade 2000). However, surveys are not completely accurate measures of predator activity, as they are conducted at varying times of day and may vary in duration across plots.

Very few nests of any shorebird species were found in the plot 14.5 km from town (n = 4), though less time was spent nest-searching here than in other plots which may have biased nest survival results. Only one nest of four was successful (one unknown, two failed), and the two failed nests were thought to be a first attempt and a re-nesting attempt by the same pair of American Golden-Plovers since they were non-overlapping in time and located 310 m apart. The low detection rate and low nest survival in this plot are somewhat surprising considering the protective potential of nesting near aggressively defensive Arctic Terns (Nguyen et al. 2006), which have been nesting there for many years (Jehl 2004). The lower apparent nesting density of shorebirds in this plot could be explained by higher predation risk due to a high density of alternative prey for foxes (goose and gull nests; McKinnon et al. 2012). As a result, shorebird nests may have been depredated before they could be found, or shorebirds have avoided this area of higher predation risk. This plot was located in close proximity to an active fox den, and there is anecdotal camera evidence that foxes passed through the plot frequently. Foxes typically re-use the same dens every year for decades if not centuries (Elmhagen et al. 2017), so it may be that shorebirds have learned to avoid nesting near dens or where predation rates are high. Indeed, this plot was identified by my data as one of higher predation risk, second only to the farthest plot from town which was near numerous active fox dens. However, it is also possible that appropriate nesting habitat is limited due to the high density of larger and/or more aggressive species which may out-compete shorebirds for nest sites.

Conclusions:

This study is the first to successfully identify predators of shorebird nests in Churchill, Manitoba using camera traps, despite decades of shorebird research conducted there. My research confirms prior findings from other Arctic sites indicating that foxes may be the most important nest predators, and therefore important determinants of predation risk and nest survival among shorebirds. Parasitic Jaegers were also documented predators and had important effects on predation risk, but effects on nest survival were not confirmed. The anthropogenic effects documented in this study were indirect in nature. Mammalian predator activity (in close proximity to nests) increased as distance to town increased, whereas for avian predators, there was no relationship found with proximity to town.

Climate change and expansion of human infrastructure in the North are ongoing processes that will continue to impact wildlife populations in the future. With climate-induced changes in habitat, primary production and predator communities in the Arctic, it is of ever-increasing importance to shorebird conservation efforts that we understand the mechanisms of their mortality at all life history stages. Animal populations are greatly determined by recruitment, and recruitment in birds can be heavily affected by changes in nest survival. In ecosystems such as the Arctic and subarctic, where predation is a main determinant of nest survival, factors affecting predation can mean the difference between a species that goes extinct and one that persists. My research, however, is just a starting point for further exploration of these subarctic ecological systems. Future studies investigating effects of predator and alternative

prey populations on shorebird nest survival should not ignore the potential direct or indirect anthropogenic effects on predator-prey interactions in Arctic and subarctic regions.

Table 1. Natural history information for study species including body mass, nest defence strategy, and average incubation duration.

Species	**Mass (g)**[1]	**Nest Defence (Predator Type)**	**Average Incubation Duration (d)**
Dunlin (*Calidris alpina*)	48-64	Distraction & concealment (avian & mammal)	20-22[1]
Short-billed Dowitcher (*Limnodromus griseus*)	90-120	Concealment (avian); distraction/retreat (mammal)	21[2]
American Golden-Plover (*Pluvialis dominica*)	100-200	Concealment (avian); distraction (mammal)	23-27[3]
Hudsonian Godwit (*Limosa haemastica*)	Females: 246-358 Males: 196-266	Concealment (avian); aggressive (avian & mammal)	22.5[4]*
Whimbrel (*Numenius phaeopus*)	310-493	Aggressive (avian & mammal)	22-28[5]

1: Warnock and Gill (1996)
2: Jehl et al. (2001)
3: Johnson et al. (2018)
4: Walker et al. (2011)
5: Skeel and Mallory (1996)
* n = 10

Table 2. Number of nests of each shorebird species found in each of four study plots, arranged by distance from human settlement (n = 50). Nests that were used in nest survival analyses are in parentheses (n = 36).

Species	**6.5 km**	**11.2 km**	**14.5 km**	**21.5 km**	**Total**
Dunlin	2 (1)	1 (1)	1 (1)	5 (4)	**9 (7)**
Whimbrel	4 (3)	8 (7)	1 (0)	7 (6)	**20 (16)**
Hudsonian Godwit	1 (1)	2 (2)	0	0	**3 (3)**
Short-billed Dowitcher	1 (1)	1 (1)	0	5 (3)	**7 (5)**
American Golden-Plover	3 (2)	1 (1)	2 (2)	0	**6 (5)**
Least Sandpiper	2 (0)	1 (0)	0	1 (0)	**4 (0)**
Stilt Sandpiper	0	0	0	1 (0)	**1 (0)**
Total	**13 (8)**	**14 (12)**	**4 (3)**	**19 (13)**	

Table 3. Twelve models of shorebird nest survival were created from combinations of five explanatory variables of interest.

	Model Name
1.	Null
2.	Fox distance
3.	Fox distance + Camera
4.	Fox distance + Species
5.	Jaeger distance
6.	Jaeger distance + Avian predator abundance
7.	Jaeger distance + Avian predator abundance + Camera
8.	Jaeger distance + Avian predator abundance + Species
9.	Jaeger distance + Fox distance + Avian predator abundance
10.	Jaeger distance + Fox distance + Avian predator abundance + Camera
11.	Jaeger distance + Fox distance + Avian Predator Abundance + Species
12.	Jaeger distance + Fox distance + Avian predator abundance + Species + Camera

Table 4. Number of avian predators observed in each of four plots of increasing distance from town, the total hours spent in each plot observing predators, and the calculated mean avian predators observed per hour. Note: because most individuals were likely nesting in the study area and observed many times over the entire season, count totals do not accurately reflect real population sizes.

Species	**6.5 km**	**11.2 km**	**14.5 km**	**21.6 km**	**Total**
Common Raven	27	37	37	11	**112**
Parasitic Jaeger	28	28	4	26	**86**
Sandhill Crane	6	26	9	29	**70**
Other	4	4	3	8	**19**
Total Predators	**65**	**95**	**53**	**74**	**287**
Total Hours	**35.02**	**48.47**	**25.80**	**60.13**	**169.42**
Mean Predators/Hour	**1.97**	**1.87**	**2.10**	**1.24**	**1.74**
SD	**0.77**	**1.06**	**1.73**	**0.62**	**1.11**
Herring Gull	105	64	295	7	**471**
Foxes	0	0	1	0	**1**
Total Predators (with gulls and fox)	**170**	**159**	**349**	**81**	**759**
Mean Predators/Hour (with gulls and fox)	**5.25**	**3.53**	**14.26**	**1.35**	**5.45**

Table 5. The best-fitting model to explain observed nest survival is the one with the lowest ΔAICc value, but any models with ΔAICc<2 (above the line) are considered competitive. In this case, because the null model falls within 2 ΔAICc, there is little support for the best-fitting model.

Model Name	**ΔAIC_c**	**No. Parameters**
Fox distance + Camera	0.000	3
Fox distance	0.469	2
Null	0.582	1
Jaeger distance	2.375	2
Jaeger distance + Avian predator abundance	2.430	3
Jaeger distance + Avian predator abundance + Camera	3.204	4
Jaeger distance + Fox distance + Avian predator abundance + Camera	3.603	5
Jaeger distance + Fox distance + Avian predator abundance	3.653	4
Fox distance + Species	8.464	6
Jaeger distance + Avian predator abundance + Species	10.531	7
Jaeger distance + Fox distance + Avian predator abundance + Species + Camera	11.045	9
Jaeger distance + Fox distance + Avian Predator Abundance + Species	11.5536	8

Table 6. Confirmed predators of artificial nests in each of four study plots, arranged by distance from human settlement.

Predator	**Distance (km)**				**Total**
	6.5	**11.2**	**14.5**	**21.6**	
Parasitic Jaeger	0	8	0	11	**19**
Arctic Fox	0	0	7	0	**7**
Herring Gull	2	1	0	0	**3**
Red Fox	1	1	0	0	**2**
Northern Harrier	0	0	1	0	**1**
Common Raven	0	0	1	0	**1**

Table 7. Confirmed predators of real shorebird nests in each of four study plots, arranged by distance from human settlement.

Predator	**Distance (km)**				**Total**
	6.5	**11.2**	**14.5**	**21.6**	
Arctic Fox	0	2	0	2	**4**
Parasitic Jaeger	0	0	0	3	**3**
Red Fox	1	2	0	0	**3**
Northern Harrier	0	1	0	0	**1**

Table 8. Frequency of nest depredation events of each focal shorebird species by each species of predator, arranged by plot in order of increasing distance from human settlement. Shorebird species codes: AMGP = American Golden-Plover; DUNL = Dunlin; SBDO = Short-billed Dowitcher; STSA = Stilt Sandpiper; WHIM = Whimbrel. An American Golden-Plover nest was depredated in the plot at 14.5 km, but the camera failed to capture any photos of the predator.

Predator	**Distance (km)**				**Total**
	6.5	**11.2**	**14.5**	**21.6**	
Arctic Fox	0	DUNL WHIM	0	WHIM[1] SBDO	**4**
Parasitic Jaeger	0	0	0	DUNL WHIM[1] STSA[3]	**3**
Red Fox	SBDO	WHIM AMGP[2]	0	0	**3**
Northern Harrier	0	AMGP[2]	0	0	**1**

[1]These two depredation events were of the same Whimbrel nest

[2]These two depredation events were of the same American Golden-Plover nest

[3]Only one Stilt Sandpiper nest was found, so it was removed from nest survival analyses

Table 9. Number of each predator type that was photographed by camera traps at randomly-placed locations in each of the four study plots.

Plot Distance (km)	Hours	Avian Predators	Foxes	Total
6.5	612	6	1	7
11.2	862	0	0	0
14.5	837	1	3	4
21.6	714	1	0	1
Total	**3025**	**8**	**4**	**12**

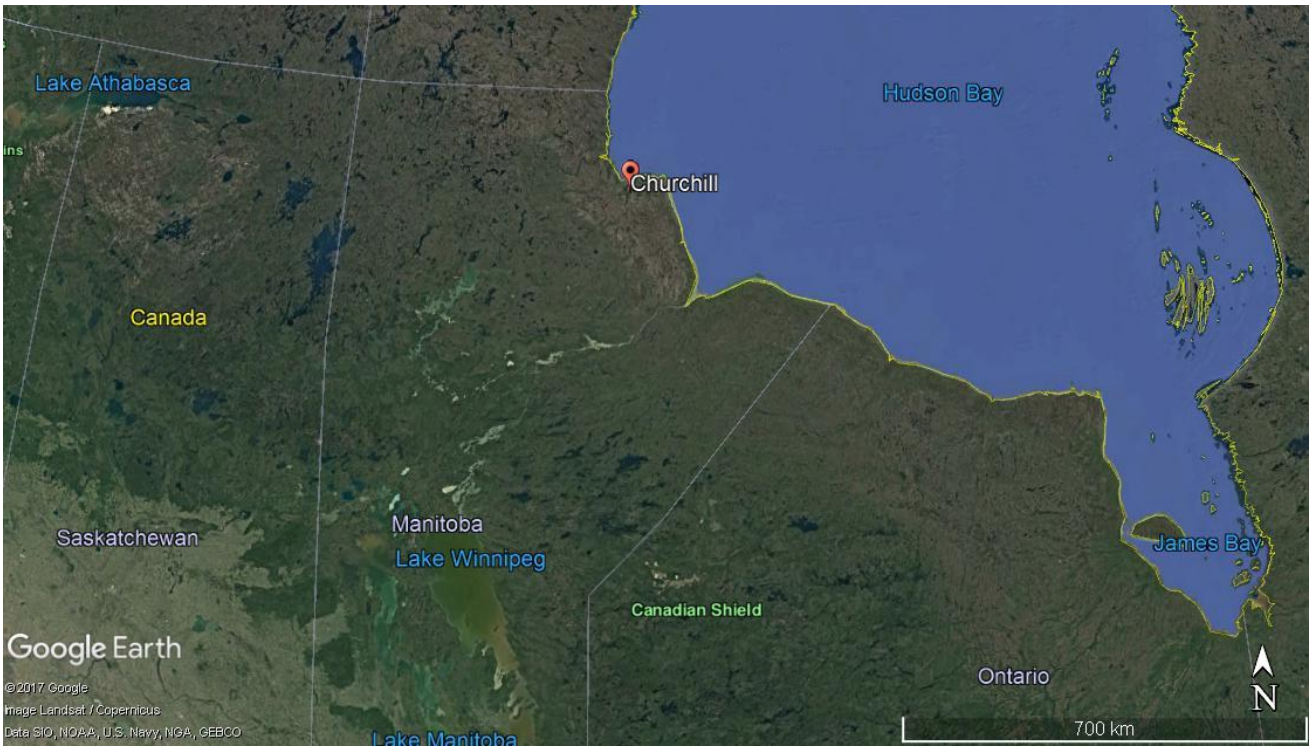

Figure 1. The study location, near Churchill, Manitoba, is situated on the west coast of Hudson Bay.

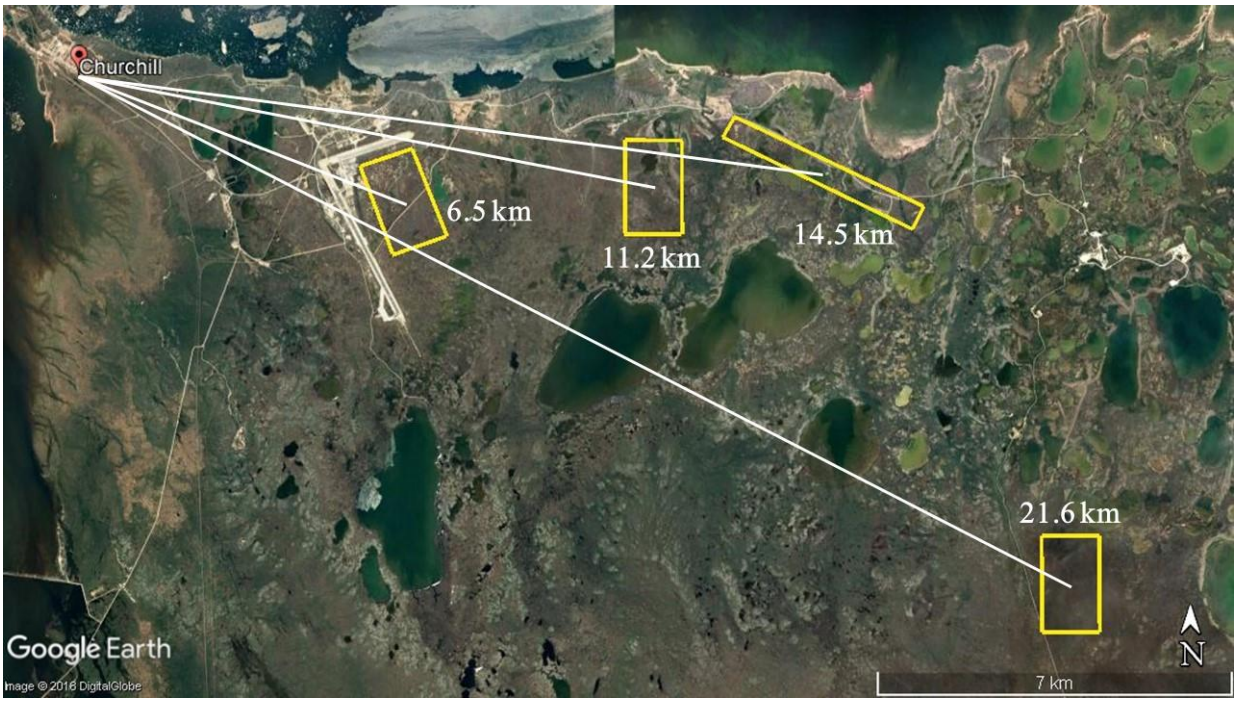

Figure 2. Four study plots, outlined in yellow, in and around the Churchill Wildlife Management Area. Each is approximately 2 km² in size. The closest plot to town is 6.5 km from the east side of town, and the most distant plot is 21.6 km from the east side of town.

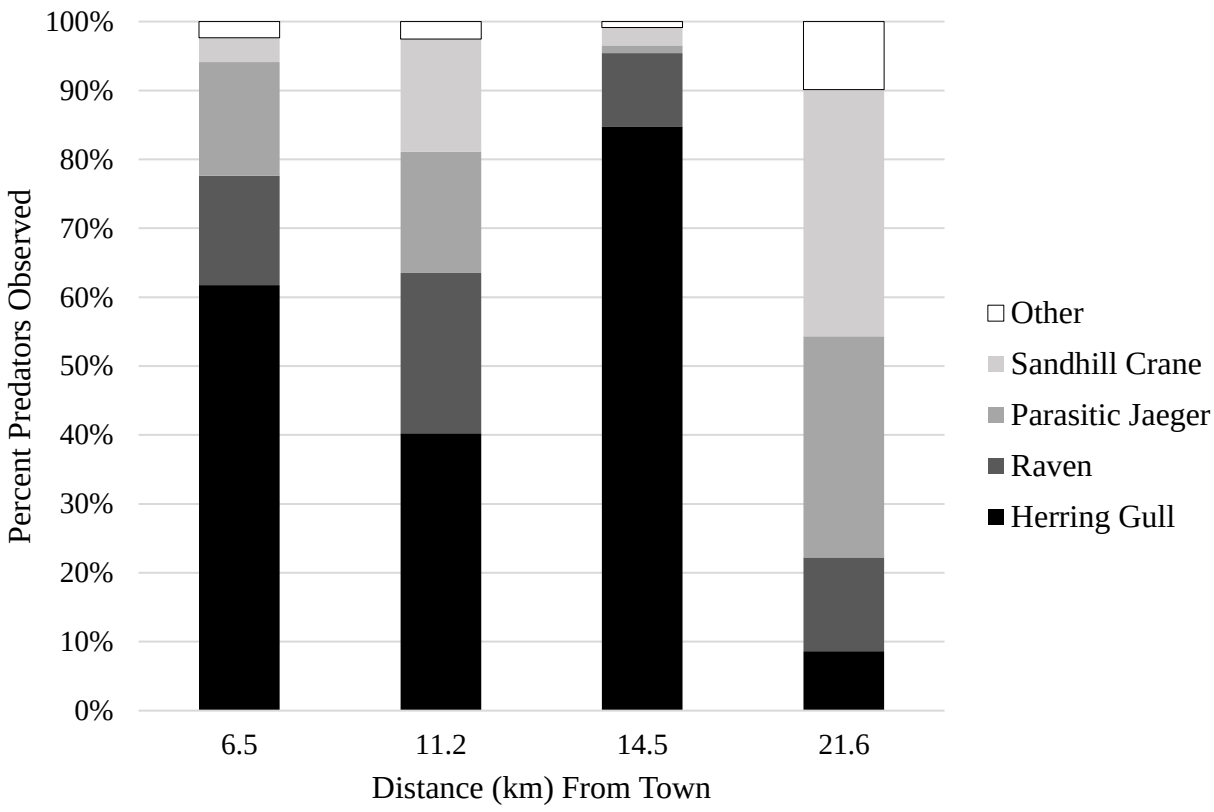

Figure 3. Proportions of avian predator species, including gulls, as observed in each of four plots of varying distance from town. "Other" predators include mostly small numbers of Harriers, Peregrine Falcons, and Bald Eagles; and, when combined with Sandhill Cranes, result in a higher diversity of predator species in the plot farthest from town.

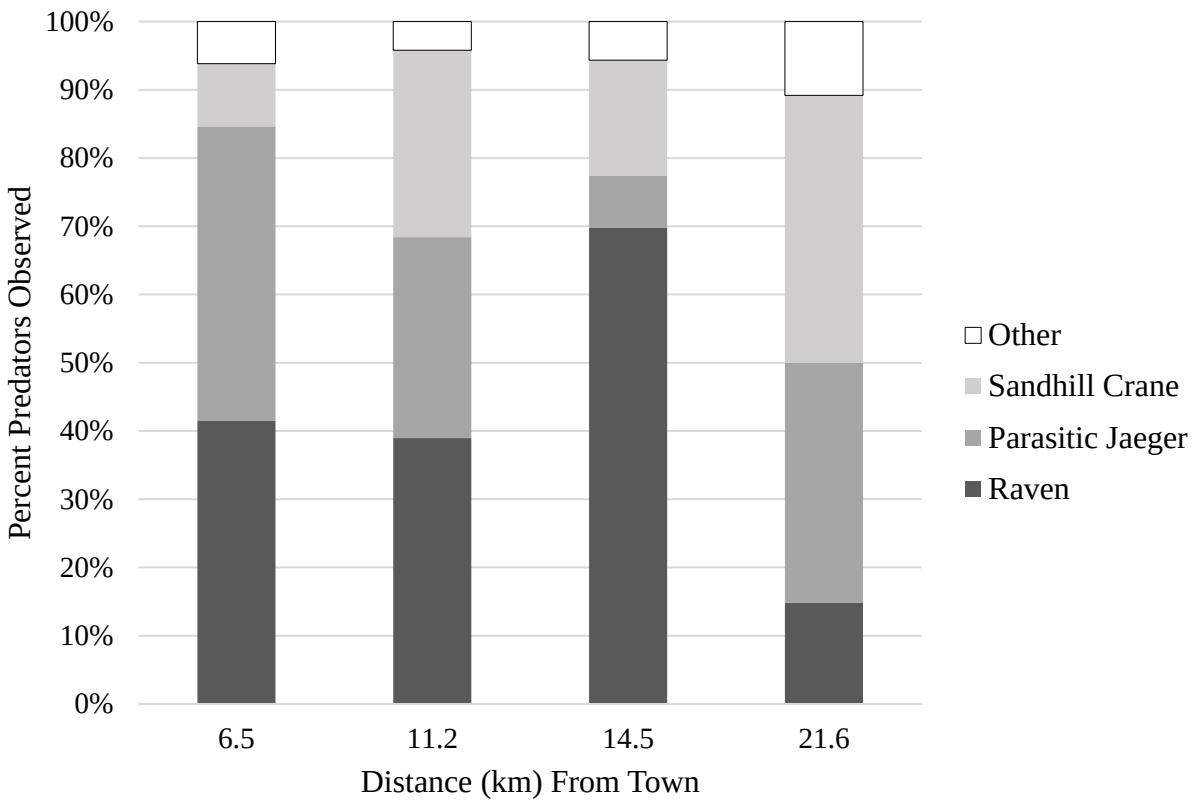

Figure 4. Proportions of avian predator species, excluding gulls, as observed in each of four plots of varying distance from town. "Other" predators include mostly small numbers of Harriers, Peregrine Falcons, and Bald Eagles; and, when combined with Sandhill Cranes, result in a higher diversity of predator species in the plot farthest from town.

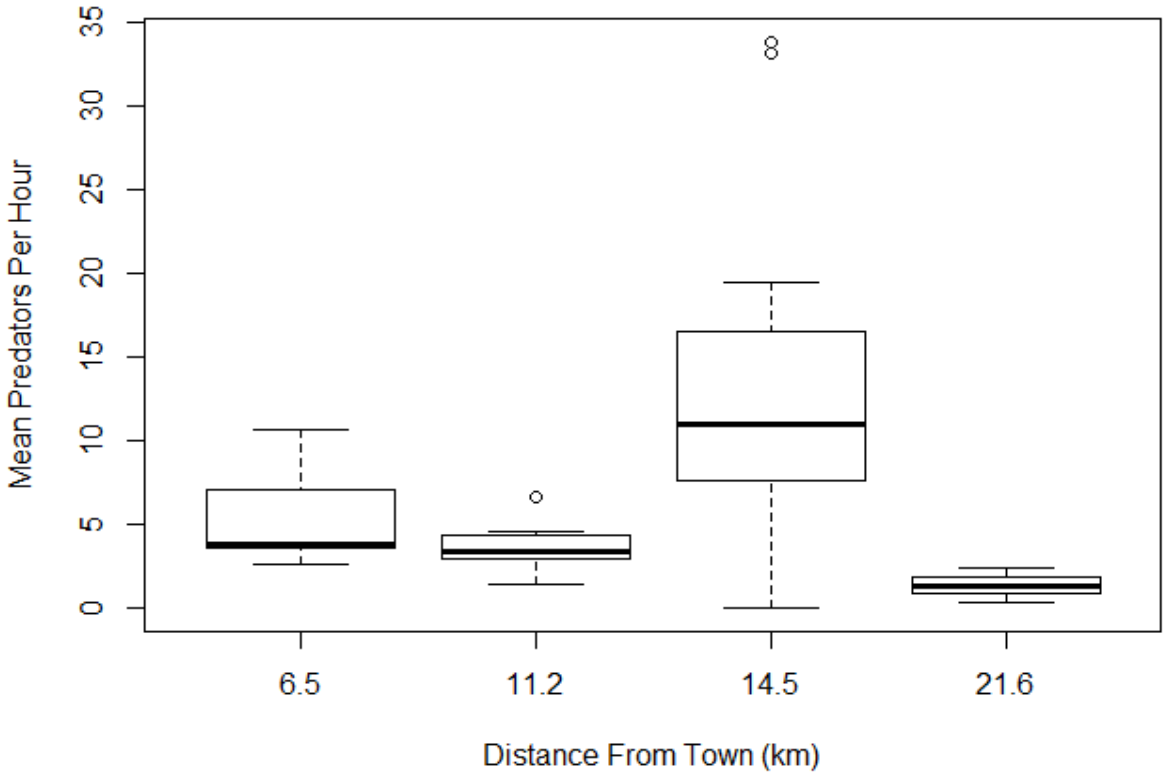

Figure 5. Mean predator abundance in each of four study plots of varying distance from town, including Herring Gulls and foxes (n = 758).

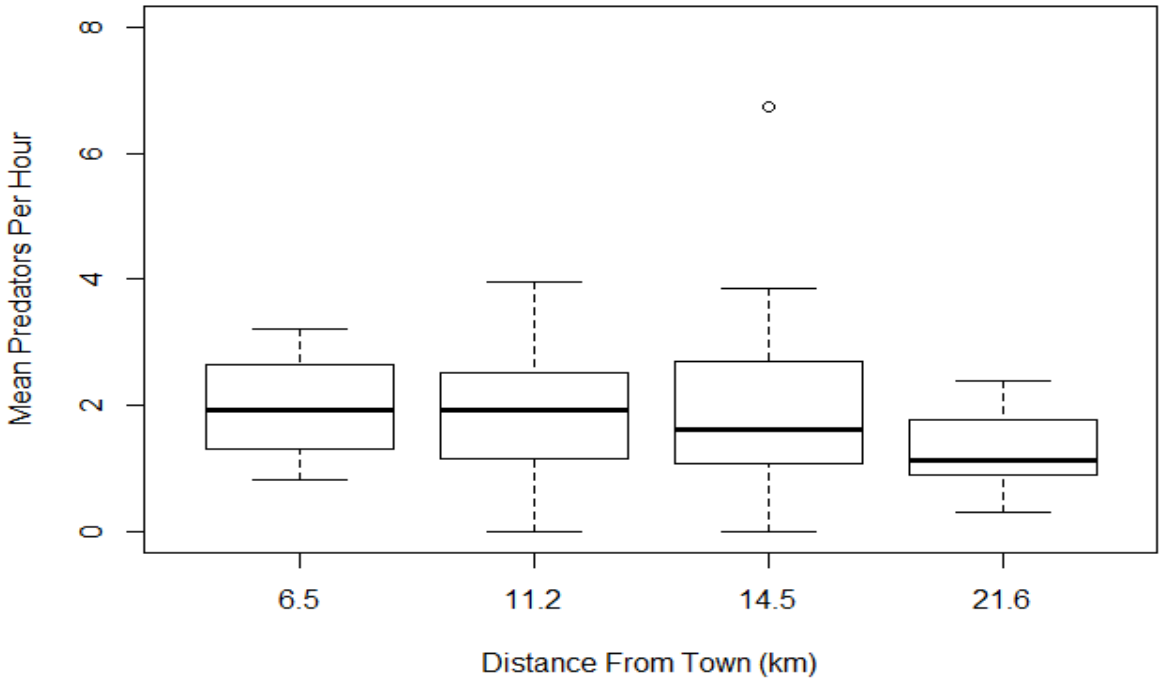

Figure 6. Mean avian predator abundance in each of four study plots of varying distance from town, excluding Herring Gulls from all plots (n = 287).

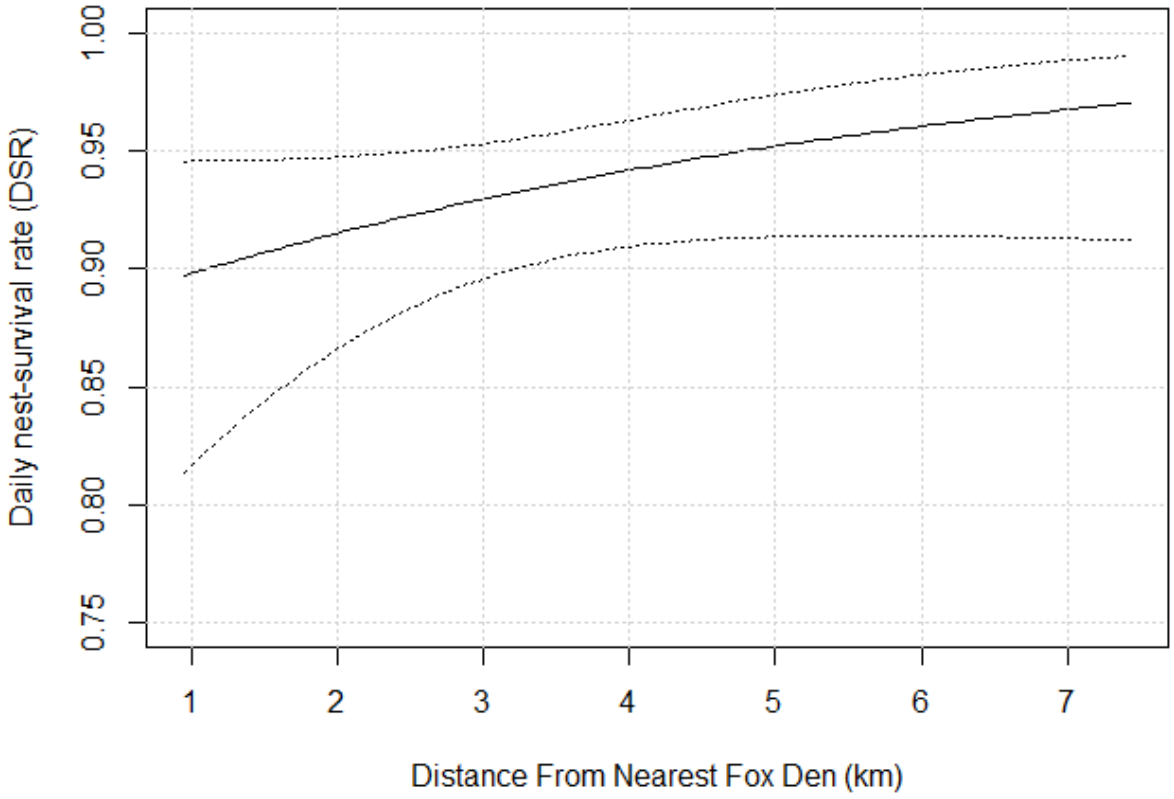

Figure 7. Daily survival rate (DSR) of shorebird nests (all species combined) near Churchill tends to increase as distance from the nearest fox den increases. Solid line is estimated DSR with dashed lines representing 95% confidence intervals.

Figure 8. Three predator species (identified with uncertainty) may have depredated a single artificial nest in the plot 11.2 km from human settlement: Arctic fox (A), Parasitic Jaeger (B), and Common Raven (C).

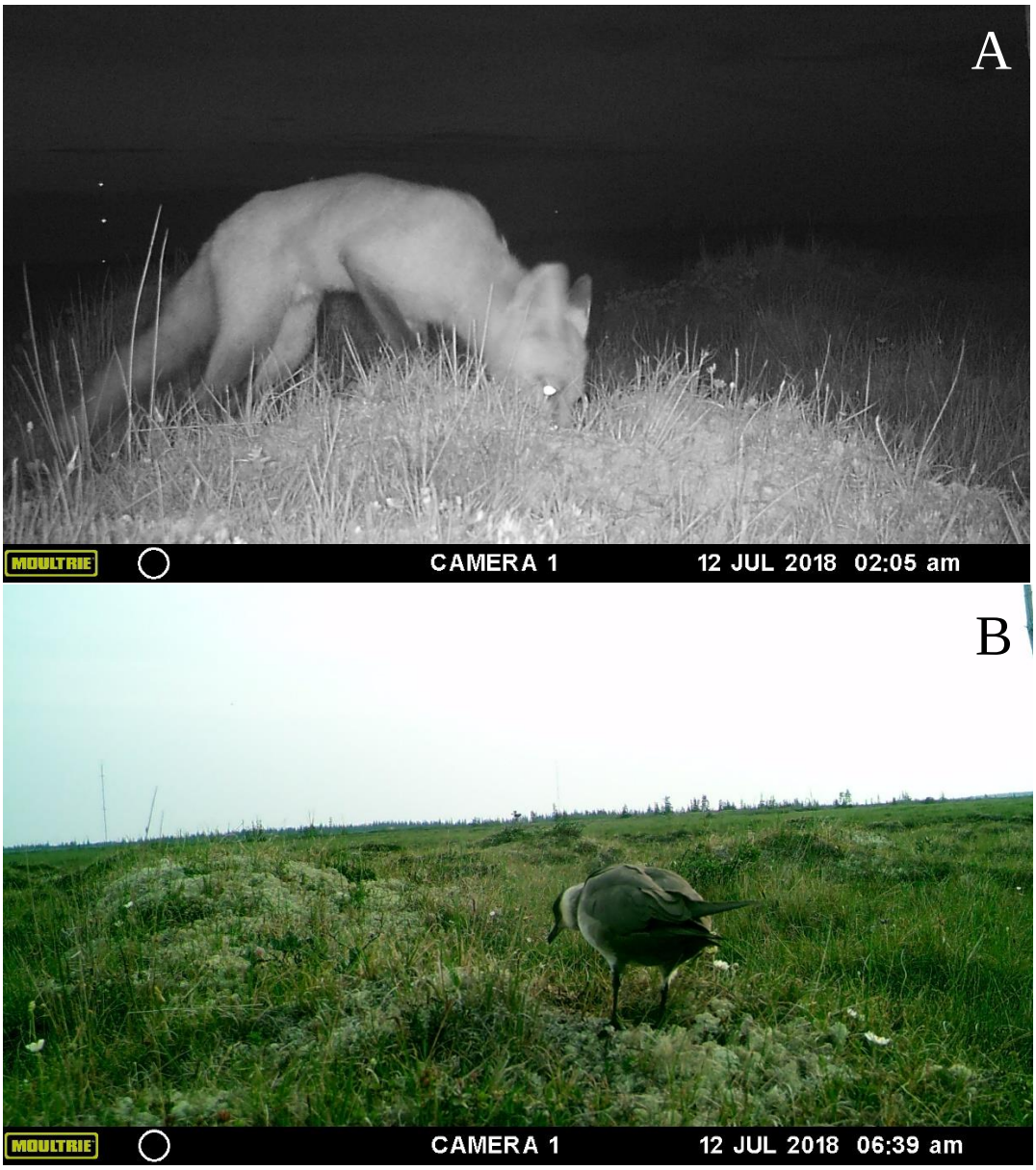

Figure 9. One artificial nest was depredated by a red fox (A), and then possibly by a Parasitic Jaeger (B).

Figure 10. One artificial nest was depredated by Parasitic Jaegers (A) and possibly by a Common Raven (B).

Figure 11. One artificial nest was depredated by a Common Raven (A), and possibly by an Arctic fox (B). Because photo sequences appear to indicate that the Raven took all four eggs from the nest, the photos of the Arctic fox with its nose in the nest cup may represent a false positive depredation event.

Figure 12. A Whimbrel nest was depredated by an Arctic fox (A) and by a Parasitic Jaeger (B).

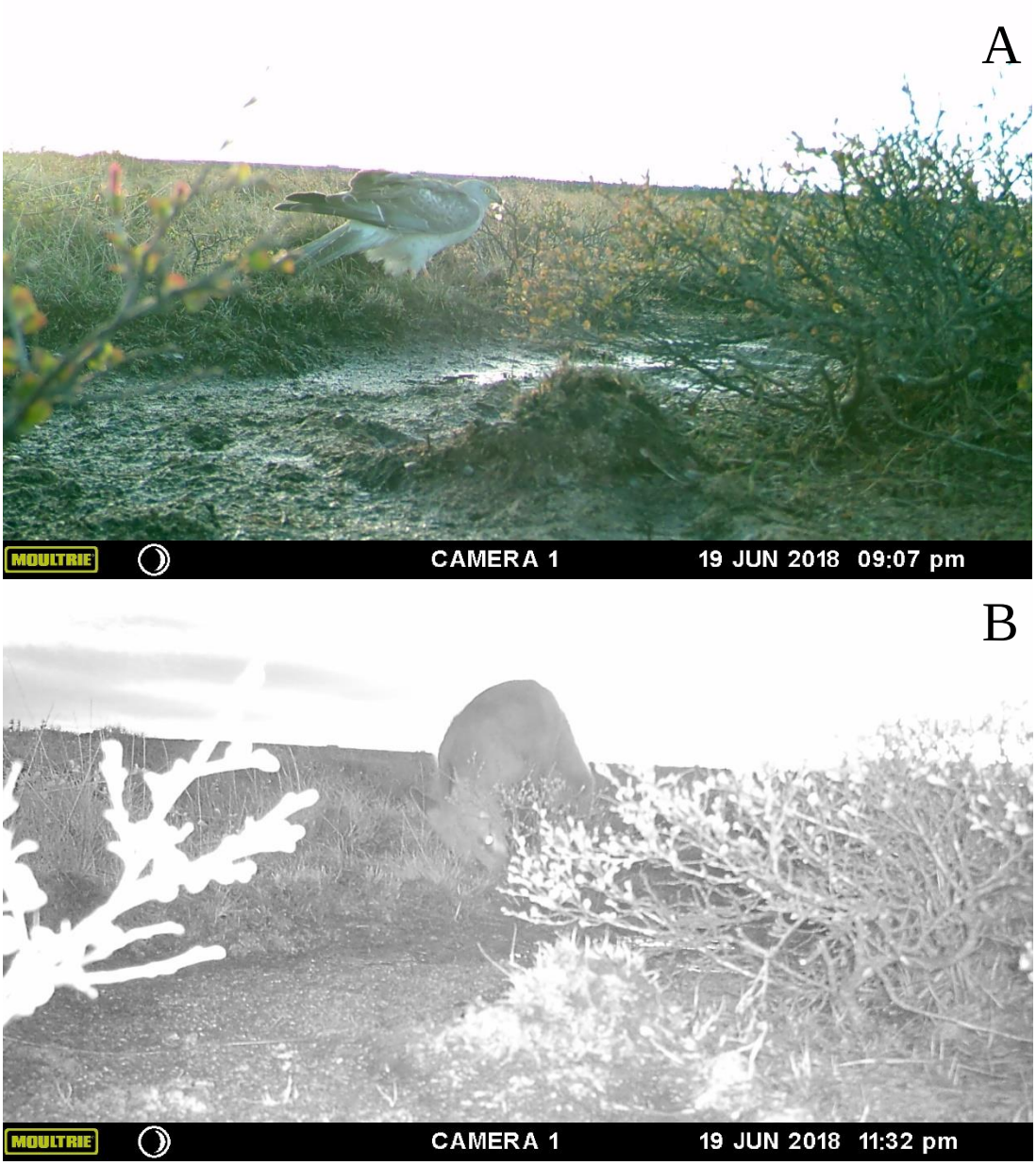

Figure 13. An American Golden-Plover nest was depredated by a Northern Harrier (A) and by a red fox (B).

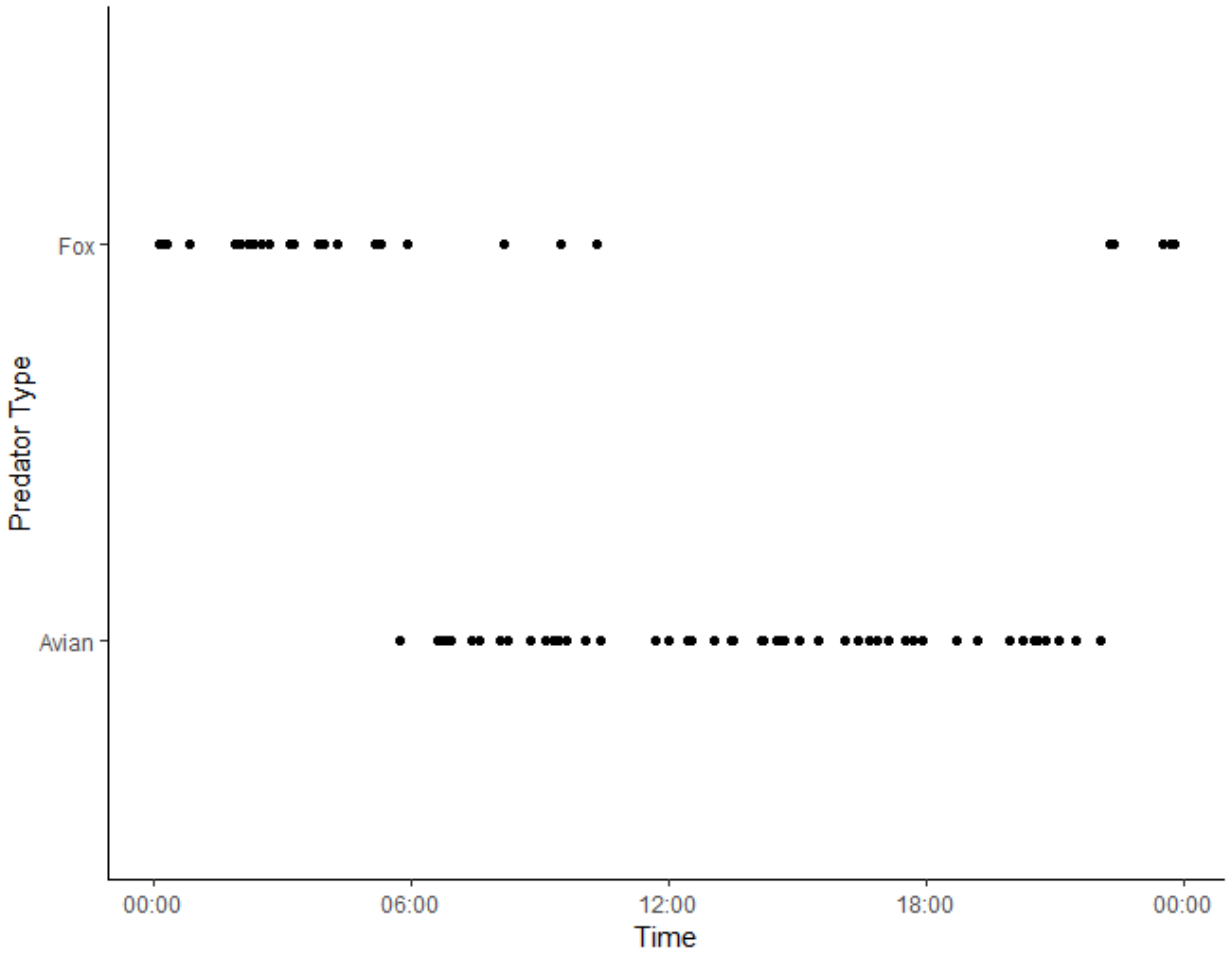

Figure 14. Types of predators detected by cameras placed at artificial and real nests and at random locations, at various times of day. Only three of thirty encounters of foxes at camera traps were outside of the hours of 22:00 – 06:00, and only three of sixty-nine encounters of avian predators at camera traps were outside of the hours of 06:00 – 22:00.

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